LYCASTIS QUADRATICEPS, AN HERMAPHRODITE NEREID WITH GIGANTIC OVA.

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The possession of unusual characters by any species or group of animals always arouses our interest and invites thorough investigation. Among the Annelida Polychæta the genus *Lycastis* in the family Nereidæ has the striking physiological peculiarity that a majority of its known species are found living in fresh water as well as in the sea — a thing of rare occurrence in other families of the Polychæta.

In addition to the above-mentioned anomaly *Lycastis quadraticeps* is an hermaphrodite; and furthermore, instead of producing many small ova it develops only a few of relatively colossal size.

The species was originally described in that comprehensive work of Claudio Gay, "Historia Fisica y Politica de Chile" ('49). The specimens are stated to have been collected at Calbuco, on the Chilean coast, and the brief description and two figures give no information beyond the diagnostic external characters. It was redescribed by de Quatrefages in 1865 (Tome II., p. 500), who, however, added nothing new.

Nearly a half century later it was rediscovered by Plate at Lapateia, Beagle Canal; and by Michaelsen, who found it at Punta Arenas, on the Straits of Magellan, living not only in the sea but in brackish water and even in fresh water; always, however, in places accessible from the sea, so that we may infer that the fresh-water habitat has been recently acquired. These observations by Plate and by Michaelsen have been recorded by Ehlers ('97, '00, and '01), who, however, failed to note the striking sexual idiosyncrasies of the species.

When, in 1902, I was engaged in the preparation of an account of certain fresh-water nereids ('03), Professor Michaelson kindly placed at my disposal a few specimens of *L. quadraticeps*. With two exceptions they proved to be sexually mature and her-

maphrodites, containing nearly ripe sperm-cells and a limited number of ova which are enormous considering the size of the parent. These facts have been already briefly recorded in the above-

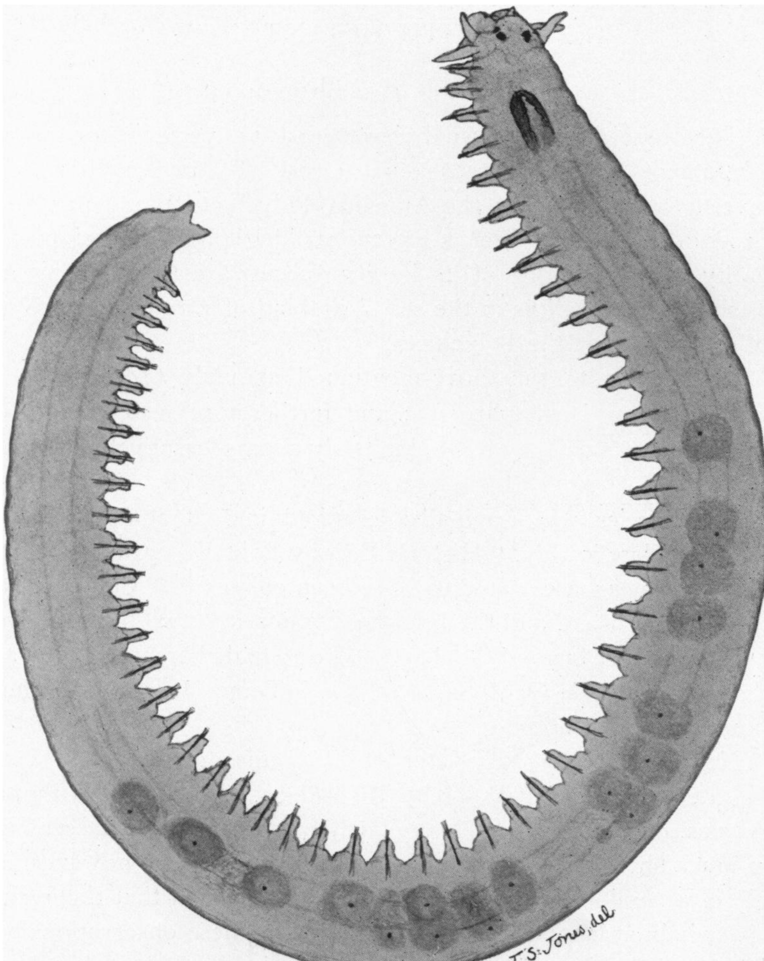

FIG. 1. *Lycastis quadraticeps* Gay. Entire worm, dorso-lateral aspect, unstained, mounted in balsam. The jaws, intestine, and large ova seen through the body-wall. Nucleoli of ova opaque and visible. $\times$ 20.

mentioned article (Johnson, '03). Since the species inhabits a region remote from ordinary travel and one cannot reasonably expect ever to see it in the living state, I have thought it worth

while to put on record the few additional facts I have been able to gather from a study of the material at hand.

The species might almost be called minute, considering the generous dimensions of most of its allies. It seldom exceeds 18 mm. in length and one millimeter in transverse diameter, including the parapodia, but not the setæ. While of a general cylindrical form and nearly uniform diameter throughout, there is a fairly marked tapering in the caudal region toward the small rounded pygidium which bears a pair of short, conical anal cirri (Fig. 1).

As in all species of *Lycastis* the feet are uniramous throughout the series, a very small tubercle and an acicula representing the dorsal ramus. The dorsal cirri differ from those of most species of the genus in being diminutive instead of large and foliaceous. Each parapod is armed with a single aristate seta representing the dorsal fascicle, and a ventral fascicle of one aristate seta and three to five falcate ones. The prostomium is characteristically short and broad; the antennæ are minute, and the tentacular cirri all short and stumpy, the stylode tapering rapidly from a short, thick ceratophore. The palpi are large for the size of the worm. The four eyes are black, those on the same side placed close together.

In specimens cleared with oil and mounted entire in balsam the internal structures can be made out in considerable detail (Figs. 1 and 2). No paragnaths have been detected, nor indeed are they known to occur in any species of Lycastis. The jaws are plainly visible and are armed with four or five teeth. The alimentary canal has the usual divisions, the only part deserving especial mention being the glandular stomach, which lies in somites VII. and VIII., or in VIII. and IX., or even extends into X. This "stomach" is thick-walled, exceeding in this respect even the œsophagus, and the lumen is strongly encroached upon by the large rounded protuberances which stud its inner surface. In sections these protuberances are seen to be composed of a syncytial mass containing numerous darkly staining nuclei, but no cell-boundaries have been detected. This is clearly a portion of the lining epithelium of the alimentary canal, but of peculiar and specialized character. In addition to the nuclei there are very many minute bodies, some round and some

elongated, which stain strongly with hæmatoxylin. The muscular layer is no thicker than in other portions of the alimentary canal.

Following the stomach is a constricted portion occupying somite IX. or X., which in turn leads directly to the intestine.

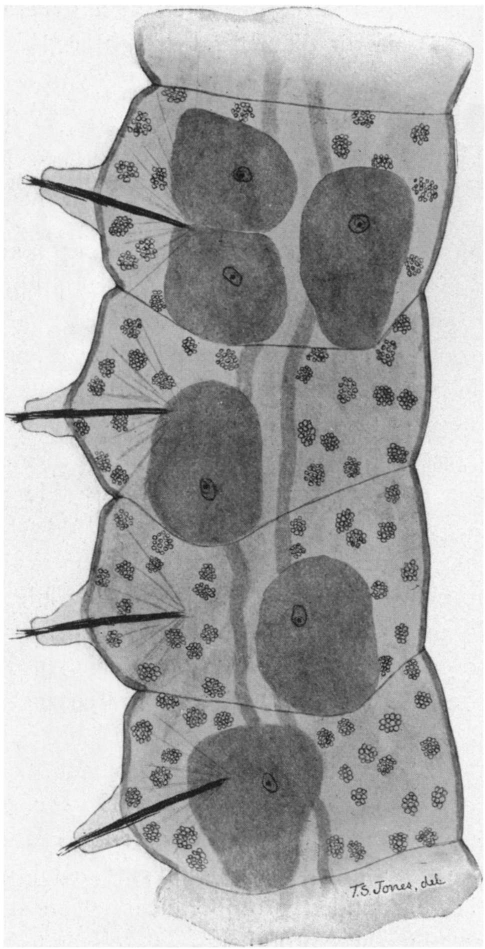

FIG. 2. Portion of another specimen, mounted in same way, more magnified. Bunches of sperm cells, ova, and intestine seen by transparency. × 37.5.

As very commonly in the Polychæta the latter is expanded in every somite and constricted at every septum. In especially well-cleared specimens a beautiful vascular network is seen to cover the peritoneal surface of the intestine.

Where one or more ripe ova occupy a somite they usually lie in contact with the digestive tube and are plainly visible as golden-yellow masses, shining through the body-wall (Figs. 1 and 2).

The sperm-cells, which are invariably in clusters, are only a little less obvious than the eggs (Fig. 2). They are present in the same somites as the ova and in many others where no ova have been found. The relations in this respect are best seen in tabular form.[1]

No. of Specimen.	Length in Millimeters.	No. of Somites.	No. of Somites with Eggs.	No. of Eggs.	No. of Somites with Sperm.	Somites without Eggs.		Somites without Sperm-cells.	
						Ant.	Post.	Ant.	Post.
1	17.3	53	20	23	36	20	9	12	7
2	19.5	56	14	16	38	16	18	12	6
3	14.4	56	18	20	43	12	20	10	7
4	17.5	61	22	32	40	16	19	14	7
5	23.0	58	30	38	42	8	8	10	8
6	13.5	45	9	9	35	12	18	7	3
7[2]	10.0	47	8?	10?	?	13	16	?	?

Inspection of the table shows that there is no fixed relation between the number of the somites and the length of the specimen, which of course has its obvious explanation in the differing degrees of contraction which the worms underwent in fixation. Nor is there a fixed relation between the total number of somites and the number of ovigerous somites, or number of ova; nor between the number of somites and the spermatogenous somites. Thus, between Nos. 5 and 6 there is a disparity of only 13 in the number of somites, but a difference of 21 in the number of their ovigerous, and of 7 in their spermatogenous, somites. The greatest disparity of all, 29, occurs in the total number of ova. Or, stated in percentages, No. 5 has about 22.4 per cent. more somites than No. 6, and 16.66 per cent. more of them produce spermatozoa; but on the other hand, No. 5 has developed over 322 per cent. more ova than No. 6! There is really more difference in size, however, than the difference in the number of the somites would indicate, amounting to 41.3 per cent. in the one dimension

[1] The counts have been made from entire specimens, usually unstained, mounted in balsam. With a species so small such preparations generally permit internal structures to be seen with admirable clearness; yet undoubtedly a few small immature ova were overlooked.

[2] Immature. Most of the ova very small, and sperm-cells not detected with certainty.

of length; hence the difference in productivity is not so great as it seems when we consider the really considerable disparity in size.

Examination of the table also shows how variable is the number of the somites, both anterior and posterior, in which neither ova nor spermatozoa develop. In general, more somites in the anterior region are destitute of sperm-cells than in the posterior, while the reverse obtains with the non-ovigerous somites. In every specimen but one (No. 5) more segments at both ends of the series are without ova than are destitute of spermatozoa; and often twice to three times as many somites contain sperm as eggs. A better balance prevails in specimen 5, which is exceptional, inasmuch as a single ovum has developed as far forward as the 9th somite, one in front of the most anterior sperm-producing one.

Many somites, even within what might be called the ovigerous series, fail to produce ova. Often the gap is only a single somite, in other places it is two, three, or more. The longest intervals have been found between the first ovum and the succeeding one (four somites in No. 2, six in No. 5). It is not improbable that a thorough study by the serial section method would bring to light minute, undeveloped ova in these apparently non-egg-bearing segments; for close inspection of the specimen mounted entire has frequently revealed small ova which were overlooked at first examination. In serial sections such ova have occasionally been found in somites packed with sperm-cells, entirely surrounded by the latter, and each accompanied by a colony of what I regard as nurse-cells (Fig. 4).

The rich golden hue of the mature ova is due to the presence of abundant yolk grains of different sizes (up to 35 microns in diameter) distributed throughout the entire ovum except a peripheral layer of finely-granular protoplasm (Figs. 3 and 5). This, however, does not appear to cover the entire ovum, being absent on the side adjacent to the intestine; but the arrangement suggests strongly that which prevails in the Arthropod egg.

The nucleus, at first very large for the size of the ovum, becomes smaller and smaller proportionally as the size of the ovum increases. (Compare Figs. 3 and 4.) The position is generally

eccentric, and the nuclear membrane is sharply defined; the chromatin, at first scanty (Fig. 4), becomes more abundant in the older eggs (Fig. 3). It has the form of granules rather than threads and sometimes part of it has a peripheral arrangement (Fig. 4).

The nucleolus at all stages of the ovum observed is a dense refractive spherical body, measuring from 10 microns in the

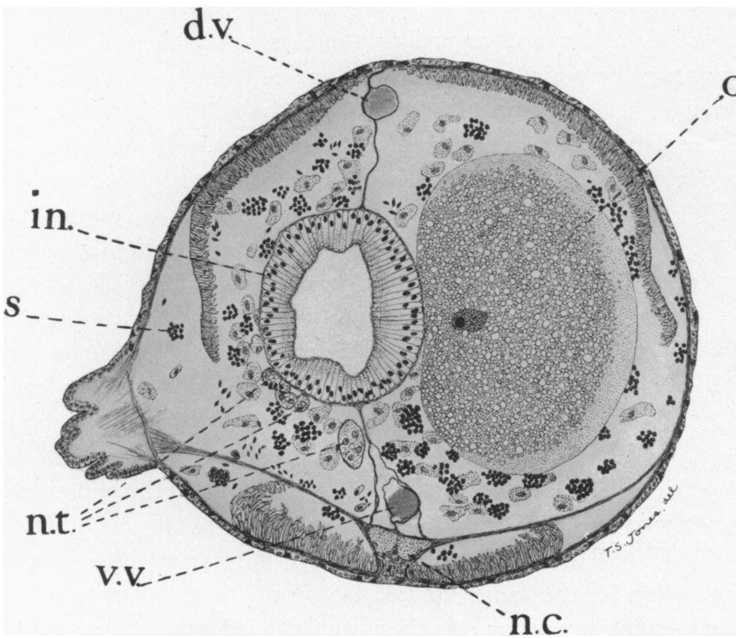

FIG. 3. Transverse section, middle region, stained with hæmalum and eosin. Section passes through an ovum (*o*) and its nucleus. Bunches of sperm cells (*s*) seen distributed throughout the cœlom. The nerve cord (*n.c.*) and transversal muscles extending from it right and left; *d.v.*, *v.v.*, dorsal and ventral blood vessels; *n.t.*, nephric tubule cut across in several places; *in.*, intestine. Amibocytes in cœlom. × 100.

young eggs up to 22 microns in the mature ones. It is eccentric in position, and remarkable for its opacity, being of a brown color by transmitted light and almost white by reflected light. Owing to the strong contrast in color to the ovum it serves as a useful landmark in the enumeration of ova.

The youngest ova and some of the mature ones are accompanied by a group of "nurse-cells." The condition, however, is

not so frequent as one would expect if every egg requires them for its proper development. It is possible there is some way of getting rid of the nurse-cells after the ova have matured, possibly by phagocytosis. This hypothesis is suggested by the fact that the bunch of nurse-cells is most commonly located in a protected place, usually in a sort of pocket between two closely-appressed ova, or between an ovum and the intestine. The aspect of the nurse-cells is closely that of young ova (Fig. 4). The principal reason indeed for not regarding them as ova is the fact that in any group there is never more than one cell that is unmistakably an ovum; it is always clearly distinguishable from the rest by greater size and the presence of yolk granules. If they were all ova one would expect a gradation from the largest to the smallest.

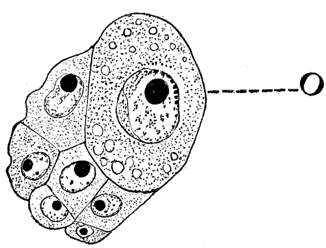

FIG. 4. Young ovum (*o*) with large nucleus, nucleolus, and a few small yolk grains. The smaller cells are considered to be nurse cells. $\times 412$.

What may be the unmodified shape of the ovum, whether spherical or oval, is impossible to determine from eggs still confined in the cœlomic spaces. In every instance owing to pressure upon each other or upon organs of the body the mature ova are more or less deformed. Pressure of the alimentary canal produces a concavity (Figs. 3 and 4); mutual pressure of two or more ova in the same somite also produces a concavity in the more yielding ovum, or else they are flattened against each other. Flattening also occurs with the largest ova where they press against the septa, extending as they do the entire distance from septum to septum. This is sometimes the case even when one or both of the adjacent somites contain no ovum, which gives the impression of unyielding septa or else of very plastic ova. The latter condition is no doubt existent. In one instance an acicula and accompanying fascicle of setæ, owing to contraction of the retractor muscles have made a deep indentation in an ovum, In other places ova are seen to be strongly constricted between two expansions of the intestine; in still other places ova are wrapped, as it were, half-way around the intestine.

Somites with two or three ova never occur near the ends of the

series but always toward the middle. Likewise, the sperm-masses are always most numerous away from the terminal somites of the spermatogenous series.

It would be instructive to compare these ova with those of other species of *Lycastis*. Unfortunately, the material is not at hand to make a general comparison ; but it may be not out of place to mention that the eggs of *Lycastis hawaiiensis* are not only much smaller (.15 mm. in diameter) but have a very different nucleus. It is one of the most beautiful examples of a naked nucleus one could expect to find. The nucleoplasm is directly and plainly continuous with the cytoplasm, and the contact of yolk-grains give the nucleus an irregular, almost stellate

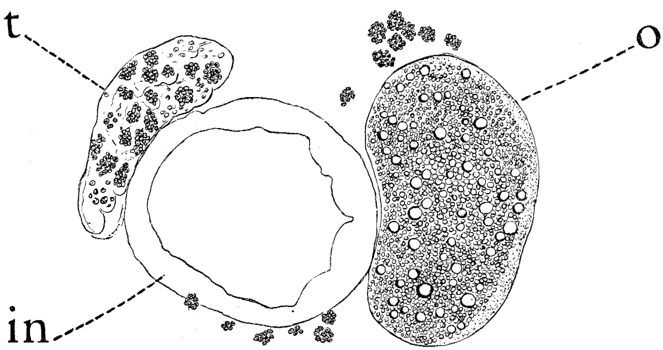

FIG. 5. Section through same specimen, and nearly same region of body, as Fig. 3. "Testis" (*t*) and ovum (*o*) appressed to the intestine (*in*). A few bunches of sperm cells (spermatocytes ?). $\times$ 112.

form. Generally there is not a single nucleolus of large size, but several small ones. No chromatic network or granules have been detected. There is no peripheral yolkless layer. In the single specimen containing ova they are very numerous, apparently nearly mature, and almost fill the cœlom of each somite. It is thus evident that within the genus *Lycastis* there are species differing widely in the structure of their ova.

None of the sectioned specimens that I have examined have ripe spermatozoa, but the sperm-cells (spermatocytes ?) present are apparently all in the same advanced stage of development. Unlike the ova, they occupy every somite from first to last of the series in which they occur, but the clusters of sperm-cells, as

appears in Fig. 3, are not limited to any particular part of the cœlom, but are loose and generally diffuse. Sometimes, however, they are massed in such a way as to give the impression of a definite organ or testis, as shown in Fig. 5. The position with relation to the ovum and intestine here shown is not constant. The spermatocytes in the "testis" are not obviously at a different stage from those free in the cœlom. This male gonad has not been found in all the specimens.

The mode of exit of the genital products offers an interesting problem. It is well-known that in many Polychæta they find their way to the outer world through the nephridia, some of which (as in *Macellicephala violacea*, recently described by Wirén, '07) may be specialized for this function. This evidently has not taken place in *Lycastis quadraticeps*. What little has been made out regarding these organs shows that they are extensive, convoluted tubules with a very narrow lumen, lying just in front of the septum of each somite (Fig. 3, *n.t.*). The lumen does not exceed in diameter one of the sperm-cells. While, so far as appearances go, it is entirely feasible for the spermatozoa to pass out through the nephridia, the same cannot be said with regard to the ova. It is obvious that they can escape only by rupture of the body-wall and consequent destruction of the parent. This is well known to be the only mode of exit in many of the Polychæta. It explains the fewness of ova in immature stages, which must in fact on this hypothesis be regarded as aborted ova, for the death of the parent in ovulation must preclude their completing their development. No immature sperm-cells have been found.

There appears to be no provision against self-fertilization, but it may nevertheless exist in the form of protandry or protogyny.

General Considerations.

Hermaphroditism among the Polychæta is of such rare occurrence that up to 1855 it was supposed to be wholly absent in the group. Even to-day, among the hundreds of known species, very many of which have been studied in their sexual phases, less than a score are known to be hermaphroditic. Although so few, the hermaphrodites are pretty well scattered throughout the entire subclass, as the following list will show. It is probably incomplete.

Macellicephala violacea (Lev.). Incipient; males and females occur. Wirén, '07.

Hesione sicula Delle Chiaje. With paired hermaphrodite organs. Bergmann, '02, '02[a].

Syllis corruscans Haswell. Anterior somites with eggs, posterior with spermatozoa. Haswell, '86; Benham, '96.

Ophriotrocha puerilis Korschelt. Protandric with hermaphrodite organs. Sexes distinguishable. Korschelt, '93; Braem, '93.

Nereis diversicolor Mueller.

Platynereis dumerili Aud. et Milne Edw. Both occasionally hermaphroditic. Caullery et Mesnil, '98.

Lycastis quadraticeps Gay.

? *Caobangia billeti* Giard. Egg-bearers only observed; male gonads not detected. Giard, '93.

Sabella microphthalmia Verrill. Protogynous paired hermaphrodite organs. Gregory, '05.

Amphiglena armandi Claparède. Ova in first ten abdominal somites; testes in last nineteen. Claparède, '64.

Salmacina dysteri (Huxley). Fissiparous. Male gonads in from three to five anterior abdominal somites; ova in eighth to twentieth. No relation between fissiparity and distribution of gonads. Huxley, '55.

S. ædificatrix Claparède. Ova in anterior abdominal somites, sperm cells in posterior ones. Claparède, '68.

S. incrustans Claparède. Claparède, '68.

Piliolaria militaris Claparède. Claparède, '68.

Spirorbis pagenstecheri Quatrefages. Pagenstecher, '63.

S. borealis. Paired gonads. Ova in first two abdominal somites; male gonads in posterior ones. Schively, '97.

S. lævis Quatrefages. Ova in first two abdominal somites, sperm-cells in all the rest. Claparède, '68.

Among Polychæta in which hermaphroditism has become established we find two distinct conditions. These occur irrespective of the systematic position of the species. In the one case male and female gonads are present in the same somite. Sometimes,

as in *Lycastis quadraticeps*, they have no discoverable relation to each other; in other forms (*Ophriotrocha puerilis*, *Hesione sicula*, *Sabella microphthalmia*), there is a definite hermaphrodite organ (Zwitterdruese). In the other and more exceptional condition the individuality of the somite asserts itself by the production of either male or female gonads. This is best seen in some of the serpulids (notably *Spirorbis*), ova alone being produced in a few of the most anterior abdominal somites, and sperm-cells in a larger number of posterior ones. It is obvious that a combination of this condition with fissiparity, if the plane of division leaves all the male gonads in one zooid and all the female gonads in the other, leads directly to an alternation of generations in which an hermaphroditic parent resolves itself into unisexual offspring. According to Haswell ('86) this actually occurs in *Syllis corruscans*, in which the anterior portion (ordinarily forming the asexual stolon in Syllids) produces ova, and the posterior somites separate as a male worm.

The ova are almost always small or even microscopic among the Polychæta. The egg of *Platynereis dumerili*, measuring .41 mm., has been regarded as one of the largest. Recently, however, Wirén ('07) has found those of Macellicephala to be much larger, and perhaps of maximum size in the entire subclass (.76 by .48 mm.). While the ova of *Lycastis quadraticeps* are not so large absolutely, measuring .43 by .28 mm., relatively to the size of the parent they are far larger.

There are at least two other species of Polychæta which produce very few relatively large ova, — *Nerilla antennata* Schmidt, '48 (*Dujardinia rotifera* of de Quatrefages, '65), and *Amphicorina cursoria* de Quatrefages, '65. Both of these species produce ova not only relatively and absolutely of unusual size, but extremely few in number (de Quatrefages's figures give six in *Amphicorina* and only four in *Nerilla*), and apparently they constitute but a single brood. In these two species therefore, we find the same condition of things as in *Lycastis quadraticeps* — reduction in the number of eggs concurrently with increase in their size — and the process has gone still further than in *Lycastis*.

That this change is not coördinate with complexity of organization or any real advance towards a higher plane of being, but

rather the reverse, is just as evident among the Polychæta as elsewhere in the animal kingdom. As the macroögenous Cladocera and Aphids occupy but a lowly position in their respective classes, and as the same is true of the auks, guillemots, and apteryx among birds, so we find the macroögenous Polychætes are all of puny size, comparatively simple organization, and one is hermaphroditic. In what, then, lies the advantage of producing so few ova? Unquestionably, there can be greater storage of food stuff per ovum if the eggs be few, and upon this the well-known law of biogenics, namely, the greater the inheritance of stored-up nutriment from the parent, the greater the chance of survival for the offspring, is based. Whether the young are launched into the world as typical, free-swimming trochophores, as modified trochophores, or in the form of young worms, has not been ascertained in any of these interesting forms. With so large a store of food-yolk a direct or nearly direct development is probable; and the very limited number of eggs presupposes such protection through the early stages that a very high percentage of the young come to maturity.

The occurrence of incipient or occasional hermaphroditism in a few species that are functionally or usually bisexual (*e. g.*, *Macellicephala violacea*, *Nereis diversicolor*, and *Platynereis dumerili*) is of especial interest. In a bisexual form like *Macellicephala* the very beginnings of hermaphroditism may be seen. According to Wirén ('07) undoubted traces of male gonads are never found in female specimens. In those which are functionally male, however, all the gonads contain groups of ova. As in the female, they are each surrounded with a follicular membrane. Free ova also occur in the cœlom, but no mature ones of full size and rounded form. It is impossible to be sure from the few observations whether this species is actually an incipient or an occasional hermaphrodite.

The most carefully-studied hermaphroditic Polychæte is probably *Ophriotrocha puerilis*. In this species, according to Korschelt ('93) it is often difficult to distinguish between males and females; but in the older specimens even in the living state the microscope reveals the ova or spermatozoa in the cœlom. Nevertheless, hermaphroditism is the prevailing condition. Says Korschelt

(p. 274): "Es kann somit kein Zweifel sein, dass bei Ophriotrocha Hermaphroditismus vorkommt und es koenne sogar maennliche und weibliche Geschlechtsprodukte zu gleicher Zeit von ein und derselben Keimdruese gebildet worden, aehnlich wie dies in der Zwitterdruese der Opisthobranchier und Pulmonaten der Fall ist."

There is a strong approach to regional hermaphroditism in Ophriotrocha. The most anterior somites of the genital series produce only male gonads and the female elements become more and more predominant towards the posterior end.

Korschelt distinguishes in Ophriotrocha four sexual phases:

1. Pure females. Male genital products not detected at any stage of development.

2. Pure males. Ova not found.

3. Apparent females. Well-developed female gonads and free ova. Also, male genital products both mature and immature.

4. Apparent males. Well-developed male gonads and multitudes of spermatozoa; ova also present in the gonads.

When both male and female elements are present in the same somite the male are found to be much further developed than the female. These individuals Korschelt believes are functionally males until the female gonads are ripe, whereupon they assume the rôle of females. There thus occurs a protandric hermaphroditism by which self-fertilization is prevented.

Something of the same nature, but with the order of events reversed, was observed by Miss Gregory ('05) in *Sabella microphthalmia.* Specimens examined in April and early part of May were pure females; in August all specimens were either hermaphrodites or females, the latter increasing in proportion as the season advanced. Pure males were not found at any time.

From the few examples that have been sufficiently studied to show the true nature of hermaphroditism in the Polychæta, it is clear that it is highly variable in its manifestations, and hardly of fixed character even in the forms where it appears to be most firmly established. This condition taken in connection with its sporadic distribution leads naturally to the conclusion that it is of comparatively recent origin in the group.

In conclusion, it is a pleasure to make grateful acknowledgment of my indebtedness to Dr. J. Percy Moore, of the University

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